

# EGG CHARACTERISTICS AND BODY RESERVES OF NEONATE ROSS' AND LESSER SNOW GEESE<sup>1</sup>

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**Abstract.** We studied the effects of species, nesting chronology and egg size on composition of eggs and goslings of Ross' (*Chen rossii*) and Lesser Snow Geese (*Chen caerulescens*). Compared to early nesters, late-nesting Ross' Geese laid eggs with less yolk protein, which in turn produced goslings with smaller pectoralis muscles. Larger pectoralis muscles of young that hatch early may enhance thermogenesis when conditions are colder. Egg composition varied isometrically with egg size. Conspecifics from larger eggs were structurally smaller for their egg size yet contained the same relative nutrient content as goslings from smaller eggs; thus goslings from larger eggs had relatively more lipid reserve. Larger egg size may give an initial energetic advantage to goslings during periods of nutritional or thermal stress. Although no interspecific variation in egg composition was observed, Ross' Geese hatched with more protein (scaled to egg size) and larger gizzards (scaled to body size). In addition, Ross' Geese had less water per gram of dry skeletal tissue mass than did Snow Geese which indicates greater functional maturity of Ross' Goose neonate tissue. Digestive efficiency, thermoregulatory ability and locomotor capacity may be relatively better in Ross' Geese than in Snow Geese and these characteristics may represent adaptations to metabolic constraints associated with smaller neonate body size and forage requirements.

**Key words:** Body size; egg size; egg composition; energetics; functional maturity; gosling composition; Lesser Snow Geese; Ross' Geese; survival.

## INTRODUCTION

Variation in egg size and composition has important implications for offspring quality in some species. Egg size can influence neonate mass (Ricklefs et al. 1978, Ankney 1980, Moss et al. 1981), survival (Parsons 1970, Nisbet 1978, Lundberg and Väisänen 1979), fasting potential (Ankney 1980, Sedinger 1986), thermal resistance (Rhymer 1988, Duncan 1988) and early growth (Schifferli 1973, Ankney 1980, Furness 1983, Peach and Thomas 1986, Larsson and Forslund 1992). Egg size generally is highly heritable (Van Noordwijk et al. 1981, Moss and Watson 1982) and, in geese, positively correlated with female body size (Newell 1988, Larsson and Forslund 1992), thus genetic factors may relate to neonate viability. Despite much previous work, the effect of egg size on offspring quality is not fully understood (Williams 1994).

Ross' (*Chen rossii*) and Lesser Snow Geese (*Chen caerulescens*, hereafter Snow Geese) often nest together in the central Canadian Arctic. As such, they experience similar local environmental conditions, e.g., weather conditions, when provisioning eggs with nutrients and rearing broods. Females rely on nutrient reserves for egg production and incubation (Ankney and MacInnes 1978) and later-nesting females may arrive with smaller reserves (see Alisauskas and Ankney 1992 for a review). Therefore, late-arriving females may reduce clutch size and/or egg quality (size/nutrient composition) to spare reserves for fasting during incubation. Clutch size declines seasonally in Ross' and Snow Geese (Ryder 1971a, 1972; Finney and Cooke 1978; Alisauskas, unpubl. data), whereas egg size does not change seasonally in Snow Geese (Newell 1988) and such information is unavailable for Ross' Geese. Also, to our knowledge, no one has examined seasonal changes in egg composition in any goose species. Nevertheless, a decline in egg

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size or quality seems maladaptive because such a trade-off could compromise offspring quality (Ankney and Bissett 1976, Ankney 1980, Lessells et al. 1989). If egg size is heritable, then lower limits to egg size should be controlled by quantity of nutrients necessary for production of viable offspring (Smith and Fretwell 1974, Brockelman 1975). Seasonal decline in growth of geese (Cooch et al. 1991, Sedinger and Flint 1991) has been attributed to seasonal variation in food availability, but egg quality may also influence early growth (Schifferli 1973, Ankney 1980, Furness 1983, Peach and Thomas 1986, Duncan 1988, Larsson and Forslund 1992).

Egg size may influence neonate energetics and, in turn, survival during nutritional or thermal stress (Ankney 1980, Alisauskas 1986, Rhymmer 1988). Mass-specific metabolic and heat loss rates are inversely related to body size (Ricklefs 1974, 1983) so, all else equal, offspring from smaller eggs use relatively more energy than those from larger eggs (*sensu* Ankney and Bissett 1976, Ankney 1980, Alisauskas 1986). During food limitation, viability of neonates should depend on relative body condition as measured by lipid to body size ratio. Goslings with more endogenous reserves relative to body size at hatch should have an energetic advantage and should survive energetic stress better than those with poorer body condition. Little is known, however, about how body size and endogenous reserves scale with increasing egg size and so the role of egg size on interspecific variation in neonate composition merits study.

Endogenous reserves of precocial neonates and ability to withstand energetically stressful conditions likely differ between Ross' and Snow Geese because adult body size and egg size are considerably smaller in Ross' Geese, about 30% and 20%, respectively (Ryder 1971b, MacInnes et al. 1989). Therefore, compared to Snow Geese, neonate Ross' Geese may be disadvantaged under poor environmental conditions (freezing temperatures, heavy precipitation) unless compensatory adaptations exist such as relatively more egg nutrients or reduced catabolism of nutrients during embryonic development which offset potential costs of smaller egg size. If Ross' Geese lay large eggs relative to their body size, then young Ross' Geese would require relatively less growth to attain adult size, representing another compensation for absolutely smaller egg size, compared to Snow Geese.

The objectives of this study were to (1) determine if egg size and egg/gosling quality changes with laying/hatching date, (2) examine the allometric relationships between egg size and gosling body size/composition, and (3) determine if Ross' Geese compensate for smaller egg size by hatching better provisioned or more developed goslings than do Snow Geese.

## STUDY AREA

Ross' and Snow Goose eggs and goslings were collected at Karrak Lake, NWT (66°15'N, 100°15'W). This colony is the largest known colony in the Queen Maud Gulf Bird Sanctuary (QMGBS) (Kerbes 1994) and contained about 364,000 geese in 1993 (Alisauskas, unpubl. data). Data were collected as part of longterm research on nesting and brood-rearing activities of geese breeding at Karrak Lake. The Karrak Lake region is a heterogenous environment with rock outcrops, sedge meadows and tundra ponds and was described by Ryder (1972).

## METHODS

### EGG AND GOSLING COLLECTION

Species of eggs collected for analysis of egg and gosling composition were determined using measurements from eggs for which species' identity was positively known. In 1992, 79 incubating Ross' and 83 Snow Geese were flushed from nests and egg length and breadth measurements were recorded (nearest 0.1 mm). Since egg size varies systematically with laying sequence (Ankney and Bissett 1976; Alisauskas, unpubl. data), only data from first eggs were used to develop criteria (Fig. 1, means (SD): Ross' length = 73.8 (2.6), width = 48.8 (1.2); Snow length = 79.6 (3.1), width = 53.1 (1.6)). Criteria for species identification (Fig. 1, Ross' length  $\leq$  73.4, width  $\leq$  49.9; Snow length  $\geq$  79.0, width  $\geq$  51.1) were then determined using means and standard deviations (SD) for length and breadth as follows.

1. Ross' Goose: length, breadth or both

$$< \bar{x}_{\text{Snow}} - 2SD_{\text{Snow}}$$

2. Snow Goose: length, breadth or both

$$> \bar{x}_{\text{Ross'}} + 2SD_{\text{Ross'}}$$

3. Unknown: both length and breadth

$$\bar{x}_{\text{Snow}} - 2SD_{\text{Snow}} < X < \bar{x}_{\text{Ross'}} + 2SD_{\text{Ross'}}$$

where X equals the egg measurement, or

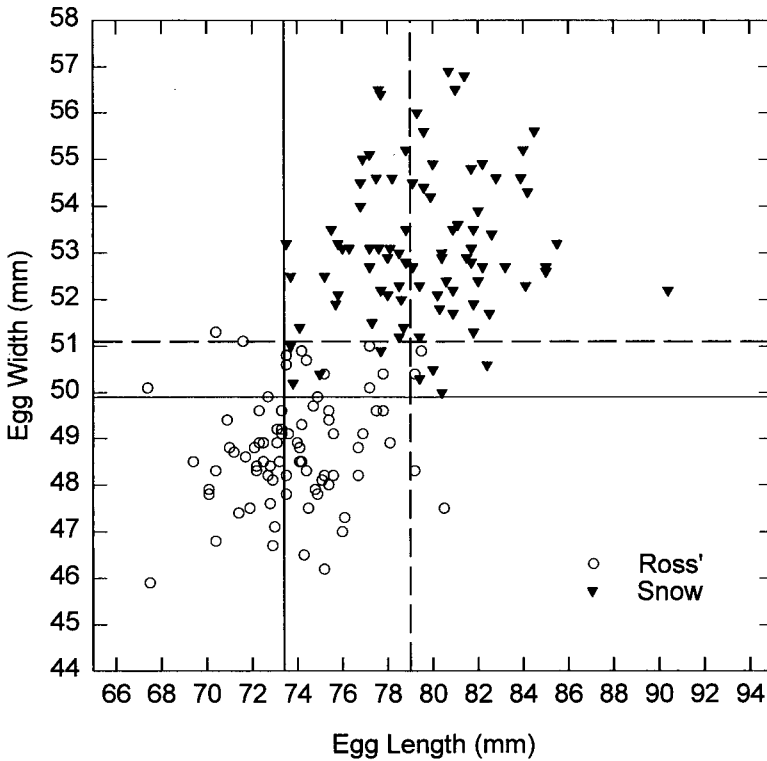


FIGURE 1. Egg size variation in known Ross' and Snow Goose eggs used to calculate criteria for determining species of study eggs. Lines represent criteria (either egg length, width or both: < solid = Ross', > dashed = Snow). Note that most interspecific variation in egg size is due to variation in egg width.

length and breadth yield conflicting species assignments.

Eggs and goslings of unknown species were deleted from analyses ( $n_{\text{eggs}} = 2$ ,  $n_{\text{goslings}} = 2$ ). Length  $\times$  breadth<sup>2</sup> (LB<sup>2</sup>) was not used because this technique resulted in more unknown eggs and goslings, likely due to the large variation in egg length for both species. We used an independent data set ( $n_{\text{Ross'}} = 46$ ,  $n_{\text{Snow}} = 48$ ) to test the accuracy of our method. Both data sets contained similar means for all species and measurement categories ( $t$ -test,  $P > 0.05$ ). We correctly classified 88% Snow and 85% Ross' Goose eggs. Only one Ross' Goose egg was misclassified as a Snow Goose egg. All other eggs were classified as unknown species.

Fresh eggs were collected from nests in center of the colony during egg laying. To reduce possible variation in composition due to position in the laying sequence, only first laid eggs were taken from each nest. Although this sampling strategy

may restrict generalizations for this population, in some species of waterfowl, egg size accounts for more variability in egg composition than does laying sequence per se (Rohwer 1986). When possible, eggs were taken from single egg nests and were assumed to be the first egg laid. However, some eggs (Ross': 12.9%; Snow: 43.9%) were removed from unincubated two and three egg clutches to better represent colony-wide clutch initiation dates. In these cases, the most heavily stained egg was assumed to have been laid first (Williams and Nelson 1943; Cooper 1978; Seding and Flint 1991, pers. observ.). Egg length and breadth were measured ( $\pm 0.1$  mm) using dial calipers and eggs were weighed ( $\pm 1.0$  g) using a digital Mettler balance. Eggs were then boiled for 20–30 min (Ankney 1980, Montevecchi et al. 1983, Birkhead 1985) and reweighed.

Goslings from pipped eggs were collected from nests in the center of the colony. Clutch size was also recorded at this time. Within clutches, the most heavily stained (i.e., the first laid) egg was

collected, then measured for length and breadth. Goslings were hatched in an incubator and weighed ( $\pm 1.0$  g) immediately after clearing the egg. After about 8 hr, dry goslings were reweighed and killed via thoracic compression (AOU 1988). Eggs/goslings were stored in sealed containers for 45 days at approximately 4°C. After returning from the Arctic, eggs and goslings were frozen at  $-10^{\circ}\text{C}$  until further processing occurred.

#### COMPOSITION ANALYSES

After thawing, each egg was separated into shell, albumen and yolk components which were then weighed to the nearest 0.001 g. Gosling midwing, tarsus, skull, culmen ( $\pm 0.1$  mm each) and body lengths ( $\pm 1.0$  mm) were measured following Dzubin and Cooch (1992). Down was plucked from goslings and right leg, right pectoralis and gizzard muscles removed and weighed separately ( $\pm 0.001$  g). Egg and gosling components were then freeze-dried to constant mass. Dry mass of components was used in subsequent analyses.

Dried albumen mass was assumed to be composed entirely of protein (Montevecchi et al. 1983). Dried yolks and goslings were analyzed for lipid and protein composition. Yolks were ground using a mortar and pestle then redried at  $90^{\circ}\text{C}$  to a constant mass and reweighed. Lipids were extracted using petroleum ether in a modified Soxhlet apparatus. Lipid-free yolk (i.e., yolk protein) samples were then redried to constant mass. Egg water content was calculated by subtracting freeze-dried egg mass from fresh egg mass. Whole dry goslings were ground using an electric blender. About 10 g of each homogenized dry gosling was redried at  $90^{\circ}\text{C}$  to constant mass. Lipids were extracted with petroleum ether using a modified Soxhlet apparatus. Lean samples were placed in a muffle furnace for 12 hr and ash was redried to constant mass and weighed. Protein was calculated by subtracting ash mass from lean mass. Water mass was calculated by subtracting freeze-dried gizzard, pectoralis, leg muscles or gosling body mass from wet mass of tissues or body mass of dry goslings 8 hr after clearing eggs, respectively.

#### STATISTICAL ANALYSES

In the following interspecific analyses, we use functional maturity of skeletal muscles (Ricklefs 1983), body size, and nutrient composition as indices of offspring quality. We predicted that

Ross' Geese have adaptations related to these measures of quality which offset potential energetic disadvantages of smaller body size. All interspecific tests are one-tailed and considered significant at  $P < 0.1$ . Where interspecific trends were opposite than predicted, we considered results significant at  $P = 0.05$ . A significance level of  $P = 0.05$  was set for all other analyses. Type III (i.e., orthogonal) sums of squares were used for all linear models (SAS Institute 1985).

*Eggs.* Unless otherwise noted, egg mass is defined as shell-free fresh mass (SHFRMASS) as determined by subtracting dried shell mass from egg mass measured before storage. SHFRMASS was used instead of fresh egg mass (FRMASS) because  $\text{LB}^2$  explained slightly more variation in SHFRMASS than in FRMASS (Table 1). Egg components were analyzed for species, laying date and egg size effects using analysis of covariance (ANCOVA) with the last two variables used as covariates. Also, analysis of variance (ANOVA) was used to test for differences in laying dates between species. To examine allometry between egg mass and egg components, we regressed the logarithm of each variable against the logarithm of egg mass (Ricklefs et al. 1978) separately for each species. Allometry was concluded if slope ( $b$ ) from log-log regression was greater than zero. Slopes equal to 1 indicate isometry (Ricklefs et al. 1978). Slopes greater than or less than one indicate a proportional increase or decrease in component with an increase in egg mass. To test for allometry of egg components, regression slopes were tested against the null hypothesis that  $b = 1$  using the test statement in Proc Reg (SAS Institute 1985). Slopes were then tested for species effects using a modified Student's  $t$ -test (Zar 1984). For all analyses involving shell, FRMASS was used instead of SHFRMASS.

Interspecific relationships between maternal body size and egg mass were determined by calculating an egg size index. Females that laid four eggs (modal clutch size; Slattery, unpubl. data) were trapped on nests during incubation. Measurements were recorded for tarsus, skull, culmen and body lengths. At this time, length and breadth were recorded for each egg in the nest. SHFRMASS was estimated from  $\text{LB}^2$  using regression equations calculated for each species from the egg composition sample (hence using known egg mass) (Table 1). We calculated the first principal component (PC1) from a principal component analysis (PCA) of maternal morpho-

TABLE 1. Parameters from simple linear regressions used to estimate fresh egg mass (FRMASS) and shell free fresh egg mass (SHFRMASS) using egg measurements ( $LB^2$  in cm).

Species	Category	$r^2$	$F$	$P$	Slope ( $b_1$ )	Intercept ( $b_0$ )
Ross' $n = 33$	SHFRMASS	0.969	958.08	<0.001	0.527	-3.163
	FRMASS	0.956	676.03	<0.001	0.565	-2.274
	Dry Shell	0.310	13.96	<0.001	0.038	0.889
Snow $n = 41$	SHFRMASS	0.949	724.65	<0.001	0.484	4.983
	FRMASS	0.948	714.67	<0.001	0.539	3.174
	Dry Shell	0.481	36.12	<0.001	0.055	-1.805

metric measurements as an index of body size (Reyment et al. 1984). Ross' and Snow Goose data were combined in the PCA so that both species were indexed on the same scale. Egg size indices were residual values calculated from a regression of clutch means for egg mass vs. female body size with data pooled across species. Interspecific variation in relative egg size was then analyzed using these residuals with ANOVA. Because all geese in this sample laid four eggs, our data are from a non-random subset of the nesting population. However, although somewhat restricted, interspecific comparisons based on maternal sample likely reflect genetic factors more than parental quality because, at least in Snow and Barnacle Geese, egg size is highly heritable (Newell 1988, Lessells et al. 1989, Larsson and Forslund 1992) and is not subject to environmental variation to the extent that clutch size is (Findlay and Cooke 1983, Newell 1988).

*Goslings.* The following analyses required calculation of egg size and body size for each gosling. SHFRMASS was estimated from  $LB^2$  for each gosling's egg from species-specific regression equations (Table 1). As an index of gosling body size, we used PC1 calculated from a PCA based on the correlation matrix of midwing, tarsus, skull, culmen and body lengths (Reyment et al. 1984), with data pooled across species. Within each species, Pearson's correlation analysis was used to determine the relationship between gosling body size and body mass. Variation in each gosling component was examined relative to species, hatch date, egg size, and body size effects using separate ANCOVA, each with one of the last three variables as the covariate. Where significant interactions existed, separate regression analyses were calculated for each species to further interpret relationships between components and the explanatory variables.

We examined relative body condition and tissue maturity for neonate Ross' and Snow Geese. Ratio of lipids:protein have been used as an index of neonate body condition (Alisauskas 1986) and the ratio of water:lean dry matter as an index of functional maturity of tissue (Ricklefs 1983, Ricklefs and Webb 1985, Konarzewski 1988, Ricklefs et al. 1994). Ratios, however, are often not normally distributed (Atchley et al. 1976, Blem 1984). Instead, we regressed lipid content of goslings against lean dry mass ( $LDM = \text{ash} + \text{protein content}$ ) and used the residuals in ANOVA to test for interspecific differences in neonate lipid reserves. To test for interspecific differences in functional maturity of muscle tissue, we calculated water content of pectoralis, leg and gizzard muscles then used ANCOVA with dry muscle mass as a covariate. Separate ANCOVA were done for each muscle tissue including skeletal muscle (dry pectoralis plus dry leg). When species by muscle tissue interactions were significant, the interactions were investigated by (1) examining species-specific slopes for water content vs. dry muscle mass and (2) comparing slopes of log-log regressions within species to determine allometric relationships between water content and dry muscle mass (Ricklefs et al. 1978).

Allometry of gosling composition was tested by regressing the logarithm of each component on the logarithm of egg size (Ricklefs et al. 1978). PC1 is a unitless measurement with a mean equal to zero and both positive and negative scores. Logarithms of negative numbers are not possible, so PC1 scores for each gosling were scaled to become positive. To do this, we used the existing eigenvectors to calculate PC1 score of a hypothetical bird of zero size, then added the absolute value of this score to the PC1 score for each gosling (Bortolotti and Iko 1992; G. Bortolotti, pers. comm.). Species were analyzed separately.

TABLE 2. Egg composition and results of ANCOVA for species and lay date effects. Partial  $F$  values are given under  $F$ .

Component	Mean (SD)		Model $r^2$	Species effect		Lay date effect	
	Ross' ( $n = 33$ )	Snow ( $n = 41$ )		$F_{1,72}$	$P$	$F_{1,72}$	$P$
Shell-free fresh egg mass (g)	84.8 (6.8)	113.1 (7.1)	0.808	256.44	<0.001	0.74	0.393
Yolk lipid (g)	12.20 (1.12)	15.74 (1.29)	0.692	129.56	<0.001	1.94	0.168
Yolk protein (g)	6.70 (0.68)	9.11 (0.68)	0.778	194.47	<0.001	5.20	0.026 <sup>a</sup>
Albumin (g)	5.72 (0.68)	7.60 (0.77)	0.625	105.12	<0.001	0.00	0.998
Total protein (g)	12.42 (1.12)	16.72 (1.02)	0.809	251.03	<0.001	2.02	0.160
Water (g)	60.11 (4.7)	80.5 (5.5)	0.795	239.32	<0.001	0.32	0.576
Shell (g)	7.21 (0.76)	10.46 (1.14)	0.732	156.41	<0.001	3.39	0.067
Lay date (June)	13.2 (2.2)	11.5 (2.8)	0.110	8.92	0.004	—	—

<sup>a</sup>  $b_1 = -0.071$ .

#### CATABOLISM OF EGG NUTRIENTS DURING EMBRYOLOGICAL DEVELOPMENT AND BODY SIZE AT HATCH

Multiple analyses of variance (MANOVA) were used to test for interspecific differences in nutrient catabolism during embryological development and structural size of neonates relative to adult size. Since mean SHFRMASS differed between egg and gosling samples (stage) for Ross' Geese ( $P < 0.05$ ), we controlled for egg size differences by dividing protein, lipid and water mass by SHFRMASS. Percentages were then arcsine-transformed (Zar 1984) and used in MANOVA. Goslings without SHFRMASS were excluded from these analyses. Data for body size MANOVA were midwing, tarsus, skull, culmen and body lengths from neonates and adults (stage). Our sample of adults were reported by Slattery (1994; Ross':  $n_{\text{males}} = 31$ ,  $n_{\text{females}} = 73$ ; Snow:  $n_{\text{males}} = 27$ ,  $n_{\text{females}} = 36$ ). For these MANOVA, we concluded an interspecific difference if species by stage interaction was significant. Relative change of mean values between stages for each nutrient or morphometric measure was then examined to determine interspecific relationships.

#### RESULTS

##### NESTING CHRONOLOGY

In 1992, mean ( $\pm$ SD) clutch initiation occurred on 13 June  $\pm 2.9$  days and 16 June  $\pm 1.9$  days while mean hatch occurred on 9 July  $\pm 2.5$  days and 12 July  $\pm 1.9$  days for Snow and Ross' Geese, respectively (Slattery and Alisauskas 1993). Mean laying dates for our egg samples were about 2 days earlier than mean initiation dates for the colony (Table 2, Ross':  $F_{\text{eggs}} = 35.68$ ,  $P_{\text{eggs}} < 0.001$ ; Snow:  $F_{\text{eggs}} = 9.18$ ,  $P_{\text{eggs}} = 0.003$ ). Mean gosling

hatch dates in our sample did not differ from those of the colony (Table 3,  $F_{\text{Ross'}} = 0.00$ ,  $P_{\text{Ross'}} = 0.976$ ;  $F_{\text{Snow}} = 0.38$ ,  $P_{\text{Snow}} = 0.537$ ). Laying and hatching dates of respective samples were normally distributed (for all tests,  $W > 0.950$ ,  $P (< W) < 0.01$ , Proc Univariate, SAS Institute 1985).

##### EGG MASS AND COMPOSITION

Snow Geese had absolutely heavier egg constituents than did Ross' Geese (Table 2). However, when controlled for egg size, no species effect was observed for any constituent (Table 4), implying the same proportional egg composition. Note, however, that trends of least square means for yolk protein and total protein were opposite than predicted and species effects were nearly significant with  $P_{\text{yolk protein}} = 0.059$  and  $P_{\text{total protein}} = 0.064$ . Yolk protein also declined seasonally in both species (Table 2). Overall, egg size accounted for greater than 80% of variation in each egg constituent (Table 4). Ross' Geese had less total protein relative to egg size than did Snow Geese (Table 4). Species  $\times$  egg size interaction, however, was significant for total protein, due to a faster rate of increase with egg size in Ross' Geese than in Snow Geese (see log-log regressions results below). For the analysis of egg size relative to female body size, residuals were derived from a significant interspecific regression of mean egg size on female body size ( $n = 71$ ,  $r^2 = 0.707$ ,  $F = 554.55$ ,  $P = 0.001$ ). No interspecific variation was observed for these residuals (Table 5) which suggests that Ross' females do not lay larger eggs for their body size than do Snow Geese.

Egg composition changed isometrically with egg mass for all constituents ( $P_{\text{slope}=1} > 0.05$ ). Total protein increased relative to egg size for Snow Geese but this trend was not significant ( $P =$

TABLE 3. Gosling composition and laying/hatching data for Ross' and Snow Geese. For simplicity, the only *F* and *P* values for the species effect presented are from ANCOVA for hatch date. Although values from ANCOVA for lay date are slightly different, patterns of significance for the species effect are similar in the lay date analyses. Degrees of freedom equal 1 for all effects. Error df equal 38 for all tests except for SHFRMASS where df equals 33. Partial *F* values are given under *F*.

Component	Ross'		Snow		Species effect		Hatch date effect		
	Mean (SD)	<i>n</i>	Mean (SD)	<i>n</i>	<i>F</i>	<i>P</i>	<i>r</i> <sup>2</sup>	<i>F</i>	<i>P</i>
Shell-free fresh egg mass (g)	89.0 (4.4)	15	109.5 (7.2)	18	88.00	<0.001	0.761	1.00	0.326
Body mass (g)	65.2 (5.0)	19	80.9 (5.6)	20	62.25	<0.001	0.699	0.32	0.574
Body size (PC1)	-0.73 (0.46)	19	0.77 (0.64)	20	52.43	<0.001	0.654	2.23	0.858
Gizzard (g)	0.54 (0.08)	19	0.67 (0.13)	20	16.54	0.001	0.317	0.03	0.144
Leg muscles (g)	0.72 (0.09)	19	0.89 (0.08)	20	25.56	<0.001	0.506	0.51	0.480
Pectoralis (g)	0.60 (0.04)	19	0.59 (0.03)	20	9.12	0.005	0.316	11.93	0.002 <sup>a</sup>
Lipid (g)	7.94 (1.13)	19	9.31 (1.02)	20	11.72	0.002	0.294	0.00	0.945
Protein (g)	10.02 (1.01)	19	12.33 (1.44)	20	26.34	<0.001	0.472	0.03	0.865
Ash (g)	1.09 (0.11)	19	1.34 (0.11)	20	39.82	<0.001	0.572	0.08	0.775
Water (g)	47.2 (3.6)	19	59.3 (3.8)	20	75.90	<0.001	0.744	0.75	0.393
Hatch date (July)	11.6 (2.1)	19	9.4 (2.4)	20	9.47	0.004	—	—	—

<sup>a</sup> Species × Hatch Date was significant (*F* = 6.57, *P* = 0.015) so separate analyses were run for each species. See text for results.

0.089). Total protein in Ross' Geese increased at a faster rate relative to egg size in Snow Geese (*t* = 2.285, *P* < 0.05, slope (95% CI): *b*<sub>Ross'</sub> = 1.09 (0.12), *b*<sub>Snow</sub> = 0.88 (0.14). We could not conclude that slopes differed interspecifically within any other component (*P* > 0.05).

GOSLING COMPOSITION

Body size and body mass were not correlated in goslings of either species (*r*<sub>Ross'</sub> = 0.347, *P* = 0.159,

*r*<sub>Snow</sub> = 0.382, *P* = 0.096). All variables were absolutely greater in Snow Geese than in Ross' Geese except for pectoralis muscle which was greater for Ross' Geese (Table 3). No seasonal effect was observed for any gosling component except pectoralis muscle (Table 3). The species-by-season interaction effect was also significant in ANCOVA including pectoralis muscle and separate regression analyses showed that declines in pectoralis muscle mass with hatch date oc-

TABLE 4. Least square means of egg components and results of ANCOVA for species effects using shell free fresh mass as a covariate. Partial *F* values are given under *F*.

Component	LS mean (SE) <sup>a</sup>		Model <i>r</i> <sup>2</sup>	Species effect		Shell free fresh egg mass	
	Ross' ( <i>n</i> = 33)	Snow ( <i>n</i> = 41)		<i>F</i> <sub>1,72</sub>	<i>P</i>	<i>F</i> <sub>1,72</sub>	<i>P</i>
Yolk lipid (g)	14.07 (0.28)	14.22 (0.24)	0.833	0.12	0.728	63.52	<0.001
Yolk protein (g)	7.75 (0.16)	8.27 (0.13)	0.873	3.84	0.051	62.33	<0.001
Albumin (g)	6.87 (0.17)	6.67 (0.14)	0.811	0.55	0.461	68.98	<0.001
Total protein (g)	14.90 (0.19)	15.10 (0.13)	0.971	5.33	0.024 <sup>b</sup>	401.84	<0.001
Water (g)	71.7 (0.3)	71.2 (0.3)	0.993	0.76	0.386	2,163.24	<0.001
Shell (g)	8.67 (0.25)	9.29 (0.21)	0.834	2.10	0.152	48.63	<0.001

<sup>a</sup> Least square means (standard error).

<sup>b</sup> Species × egg size interaction significant (*F* = 4.44, *P* = 0.039). Slopes for species-specific (SD of estimate) regressions of total protein with shell free fresh mass: *b*<sub>Ross'</sub> = 0.158 (0.009), *b*<sub>Snow</sub> = 0.128 (0.010). See text for discussion.

TABLE 5. Indices for egg size relative to adult female body size, neonate body condition, and functional maturity of tissues. A lower LS mean value for muscle water indicates greater functional maturity of tissue. Interspecific tests are one-tailed.

Index	LS Mean (SE)				Model <i>r</i> <sup>2</sup>	Species effect		Muscle tissue effect	
	Ross <sup>a</sup>	<i>n</i>	Snow	<i>n</i>		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Egg size <sup>a</sup>	-0.58 (0.64)	47	0.88 (0.80)	24	0.010	2.03 <sup>b</sup>	0.156	—	—
Lipid <sup>c</sup>	-0.04 (0.20)	19	0.04 (0.20)	20	0.002	0.08	0.785	—	—
Muscle water									
Skeletal	2.31 (0.04)	19	2.45 (0.04)	20	0.842	4.34	0.044	78.20	0.0001
Pectoralis	0.30 (0.01)	19	0.35 (0.01)	20	0.786	7.93	0.008 <sup>d</sup>	111.20	0.0001
Leg	2.01 (0.04)	19	2.11 (0.04)	20	0.866	2.99	0.092	90.71	0.0001
Gizzard	2.39 (0.03)	19	2.36 (0.03)	20	0.923	0.36	0.550	322.92	0.0001

<sup>a</sup> Residuals from regression analyses of egg mass on body size of parent females. Data from females laying four egg clutches.  
<sup>b</sup> *F*<sub>1,60</sub>.  
<sup>c</sup> Residuals calculated from a regression of lipid on LDM.  
<sup>d</sup> Species × pectoralis interaction significant, *F* = 14.76, *P* = 0.0005, slopes (SD of estimate) for species-specific regressions of water content with dry pectoralis mass: *b*<sub>Ross</sub> = 1.87 (0.41), *b*<sub>Snow</sub> = 4.02 (0.37). See text for discussion.

curred only in Ross' Geese (Ross', *n* = 18, *r*<sup>2</sup> = 0.523, *b* = -0.015, *t* = -4.176, *P* < 0.001; Snow, *n* = 20, *r*<sup>2</sup> = 0.016, *b* = -0.002, *t* = -0.539, *P* = 0.597).

Interspecific regressions of lipid on LDM (condition index) used to produce residuals for subsequent analyses were significant (*r*<sup>2</sup> = 0.538, *F* = 43.09, *df* = 1, *P* = 0.0001). Although an interspecific difference in body condition (lipid) index was not observed, Ross' Goose neonate skeletal muscle tissue contained less water than that of Snow Geese (*P* = 0.044, Table 5), suggesting greater functional maturity (Ricklefs and Webb 1985, Konarzewski 1988, Ricklefs et al. 1994). Gizzard tissue contained relatively similar amounts of water. For pectoralis, species by tissue interaction was significant (*P* = 0.0005, Table 5) and log water-log dry pectoralis regression analysis demonstrated that proportional decrease in functional maturity with increased tissue dry mass occurred at a slower rate in Ross' Geese than in Snow Geese (log-log regressions, Ross': *r*<sup>2</sup> = 0.54, *b*<sub>1</sub> = 0.63 (SE = 0.14), *F*<sub>*b*<sub>1=0</sub></sub> = 4.44, *P*<sub>*b*<sub>1=0</sub></sub> = 0.0004, *F*<sub>*b*<sub>1=1</sub></sub> = 6.62, *P*<sub>*b*<sub>1=1</sub></sub> = 0.02; Snow: *r*<sup>2</sup> = 0.89, *b*<sub>1</sub> = 1.17 (0.1), *F*<sub>*b*<sub>1=0</sub></sub> = 11.81, *P*<sub>*b*<sub>1=0</sub></sub> = 0.0001, *F*<sub>*b*<sub>1=1</sub></sub> = 3.14, *P*<sub>*b*<sub>1=1</sub></sub> = 0.093; ANCOVA statistics for species × pectoralis interaction indicating interspecific difference in slopes: *F* = 9.73, *df* = 1, *P* = 0.004).

Results from ANCOVA using SHFRMASS showed that all gosling components except leg

and pectoralis muscles were correlated with egg mass (Table 6). When controlled for differences in egg mass, Ross' Geese had relatively more protein and ash and smaller body size than did Snow Geese. Mass for all other components did not differ interspecifically. In addition, egg mass accounted for more variation in neonate body mass than in body size (Table 6).

Accounting for differences in neonate body size, Ross' Geese had relatively lighter body mass and less water, but heavier gizzards than did Snow Geese (Table 7). In addition, Snow Geese had more lipids but small sample sizes (*n*<sub>Ross</sub> = 15, *n*<sub>Snow</sub> = 18) could have precluded detection of a significant difference (*P* = 0.075, two-tailed since the relationship is opposite than predicted). No other differences between species were observed. Interspecific variation in body mass was likely due to relative differences in water content. All components were positively correlated with body size except pectoralis muscle and lipid content (Table 7).

Snow Geese that hatched from heavier eggs were relatively smaller and had relatively more protein than those hatching from lighter eggs (Table 8). Log-log regression of body size on egg size was nearly significant in Ross' Geese (Table 8, 0.05 < *P*<sub>*b*<sub>0</sub></sub> < 0.1, *P*<sub>*b*<sub>1</sub></sub> < 0.001) and detection of a relationship likely was impaired by small sample size (*n* = 15). No relationship with increasing egg size was observed for leg or pector-



TABLE 6. Interspecific differences in gosling composition using ANCOVA with SHFRMASS as a covariate. Sample sizes:  $n_{\text{Ross}} = 15$ ,  $n_{\text{Snow}} = 18$ . Partial  $F$  values are given under  $F$ .

Component	LS means (SE) <sup>a</sup>		Model $r^2$	Species effect		Shell free fresh egg mass effect	
	Ross <sup>c</sup>	Snow		$F_{1,32}$	$P$	$F_{1,32}$	$P$
Body mass (g)	74.3 (0.9)	73.8 (0.8)	0.937	0.11	0.745	120.97	<0.001
Body size (PC1)	-0.22 (0.22)	0.41 (0.19)	0.724	3.08	0.090	8.31	0.007
Gizzard (g)	0.64 (0.04)	0.59 (0.04)	0.415	0.52	0.476	8.59	0.006
Leg muscles (g)	0.77 (0.03)	0.86 (0.03)	0.538	2.16	0.151	2.63	0.115
Pectoralis (g)	0.60 (0.01)	0.59 (0.01)	0.031	0.59	0.450	0.95	0.337
Lipid (g)	9.01 (0.38)	8.44 (0.34)	0.434	0.80	0.378	9.97	0.004
Protein (g)	12.06 (0.27)	10.73 (0.25)	0.834	8.04	0.008	72.35	<0.001
Ash (g) <sup>b</sup>	1.28 (0.03)	1.17 (0.02)	0.863	4.07	0.052	72.32	<0.001
Water (g)	53.2 (0.80)	54.6 (0.73)	0.917	1.03	0.318	68.87	<0.001

<sup>a</sup> Least squares means (standard error).  
<sup>b</sup> Fresh egg mass used for analysis.

alis muscles. All other components varied isometrically with egg size (Table 8). The regression line for Ross' Goose gizzard is only marginally significant ( $P_{b=0} = 0.057$ ) but this is likely due to small sample size ( $n = 15$ ). We found no interspecific variation in log-log slopes for any component, although protein was marginally different ( $0.05 < P < 0.1$ ;  $b_{\text{Ross}} < b_{\text{Snow}}$ ).

CATABOLISM OF EGG NUTRIENTS DURING EMBRYONIC DEVELOPMENT AND BODY SIZE AT HATCH

No interspecific difference was observed for catabolism of nutrients by embryos (MANOVA,  $P > 0.05$ , Table 9). Note, however, that the ANOVA for protein consumption was significant (2.9%

TABLE 7. Interspecific variation in gosling composition using ANCOVA with body size (PC1) as a covariate. Sample sizes:  $n_{\text{Ross}} = 15$ ,  $n_{\text{Snow}} = 18$ . Partial  $F$  values are given under  $F$ .

Component	LS means (SE) <sup>a</sup>		Model $r^2$	Species effect		Body size effect	
	Ross <sup>c</sup>	Snow		$F_{1,32}$	$P$	$F_{1,32}$	$P$
Body mass (g)	69.2 (1.72)	78.7 (1.50)	0.724	11.85	<0.001	4.33	0.046
Gizzard (g)	0.68 (0.03)	0.58 (0.02)	0.660	5.36	0.028	38.21	<0.001
Leg muscles (g)	0.79 (0.03)	0.85 (0.02)	0.593	1.53	0.226	8.19	0.008
Pectoralis (g)	0.60 (0.01)	0.59 (0.01)	0.030	0.15	0.697	0.70	0.409
Lipid (g)	8.08 (0.40)	9.27 (0.35)	0.243	3.40	0.075	0.00	0.999
Protein (g)	11.07 (0.41)	11.68 (0.35)	0.553	0.84	0.367	8.06	0.008
Ash (g)	1.22 (0.03)	1.24 (0.03)	0.739	0.48	0.484	24.08	<0.001
Water (g)	50.0 (1.19)	57.7 (1.04)	0.760	16.19	<0.001	4.11	0.052

<sup>a</sup> Least squares means (standard error).

TABLE 8. Allometric relationships of gosling composition with shell free fresh egg mass. Slopes are calculated from the regression of log component on log shell free fresh egg mass.

Species	Component	<i>b</i>	95% CL (±)	<i>r</i> <sup>2</sup>	<i>t</i> <sub><i>b</i>-0</sub>	<i>P</i> <sub><i>b</i>-0</sub>	<i>F</i> <sub><i>b</i>-1</sub>	<i>P</i> <sub><i>b</i>-1</sub>
Ross' ( <i>n</i> = 15)	Body mass	1.044	0.265	0.848	8.521	<0.001	0.129	0.726
	Body size	0.275	0.331	0.199	1.798	0.095	22.412	<0.001
	Gizzard	1.073	1.116	0.249	2.078	0.058	0.020	0.890
	Leg muscles	0.358	1.411	0.023	0.548	0.593	0.965	0.344
	Pectoralis	-0.114	0.750	0.008	-0.328	0.748	10.301	0.007
	Lipid	1.484	1.461	0.270	2.194	0.047	0.513	0.487
	Protein	0.967	0.676	0.424	3.092	0.009	0.011	0.918
	Ash	1.511	0.645	0.663	5.058	<0.001	2.925	0.111
	Water	0.986	0.398	0.688	5.350	<0.001	0.006	0.941
Snow ( <i>n</i> = 18)	Body mass	0.946	0.267	0.780	7.523	<0.001	0.182	0.624
	Body size	0.313	0.293	0.242	2.263	0.038	24.648	<0.001
	Gizzard	1.530	1.474	0.232	2.200	0.043	0.581	0.457
	Leg muscles	0.567	0.685	0.161	1.753	0.099	1.797	0.199
	Pectoralis	0.326	0.378	0.173	1.826	0.087	14.288	0.002
	Lipid	0.821	0.760	0.247	2.291	0.036	0.249	0.624
	Protein	1.647	0.480	0.768	7.270	<0.001	8.161	0.011
	Ash	1.171	0.350	0.759	7.099	<0.001	1.072	0.316
	Water	0.826	0.284	0.704	6.166	<0.001	1.685	0.213

difference, Ross' < Snow, *P* = 0.072, one-tailed test, Table 9).

The ratio of adult size : gosling size can be considered the "growth increment needed to attain adult size" (Alisauskas 1986). When gosling morphometrics were compared to the sample of adults used in Slattery (1994), Ross' Geese needed about 12% less incremental growth to reach adult size than did Snow Geese (*P* < 0.05, Table 10). Overall, goslings hatched with small midwings and large tarsi relative to other morphometric features.

DISCUSSION

SEASONAL EFFECTS ON EGG AND GOSLING COMPOSITION

In both Ross' and Snow Geese, clutch size declines seasonally (Ryder 1972; Finney and Cooke

1978; Alisauskas, unpubl. data), presumably because birds that nest later have fewer nutrient reserves to allocate to egg production than birds that nest earlier (see Alisauskas and Ankney 1992 for a review). Clutch size in Snow Geese shows no heritability (Findlay and Cooke 1983) and thus all variation is environmentally induced. Egg size in geese, however, is both highly heritable and repeatable (Newell 1988, Larsson and Forslund 1992). Ankney and Bissett (1976), Rohwer and Eisenhauer (1989) and Lessells et al. (1989) all examined the relationship between

TABLE 10. Growth increment of morphometric measurements in Ross' and Snow Goose goslings. Difference significant (MANOVA, *F*<sub>5,199</sub> = 80.4, *P* = 0.0001).

Species	Component	Mean length (mm)		Growth increment <sup>c</sup>	% Difference <sup>d</sup>
		Goslings <sup>a</sup>	Adults <sup>b</sup>		
Ross'	Midwing	17.4	133.4	7.6	9.5
	Tarsus	29.3	68.7	2.3	8.0
	Skull	38.5	84.9	2.2	15.4
	Culmen	14.6	40.2	2.8	15.2
	Body	149.2	473.6	3.2	11.1
Snow	Midwing	18.6	156.8	8.4	
	Tarsus	32.1	82.7	2.5	
	Skull	43.2	113.6	2.6	
	Culmen	17.1	55.8	3.3	
	Body	163.2	581.2	3.6	

<sup>a</sup> Sample sizes: *n*<sub>Ross'</sub> = 19, *n*<sub>Snow</sub> = 20.  
<sup>b</sup> Sample sizes: *n*<sub>Ross'</sub> = 104, *n*<sub>Snow</sub> = 63.  
<sup>c</sup> Adult length/Gosling length.  
<sup>d</sup> [(GI<sub>Snow</sub> - GI<sub>Ross'</sub>) / GI<sub>Snow</sub>] × 100%.

TABLE 9. Percent change in nutrient composition during embryological development. Values represent the percentage of nutrients catabolized by embryo during incubation. Statistics are for one-tailed test of species × stage interaction. MANOVA non-significant, *F*<sub>3,102</sub> = 1.52, *P* = 0.213.

Component	Ross'	Snow	Snow-Ross'	<i>F</i> <sub>3,104</sub>	<i>P</i>
Lipid	-36.8 <sup>a</sup>	-38.8	1.9	0.45	0.502
Protein	-29.5	-32.4	2.9	3.30	0.072
Water	-23.7	-24.0	0.3	0.16	0.687

<sup>a</sup> [(mean % of component in SHFRMASS<sub>egg</sub> - mean % of component in SHFRMASS<sub>gosling</sub>) / (mean % of component in SHFRMASS<sub>egg</sub>)].

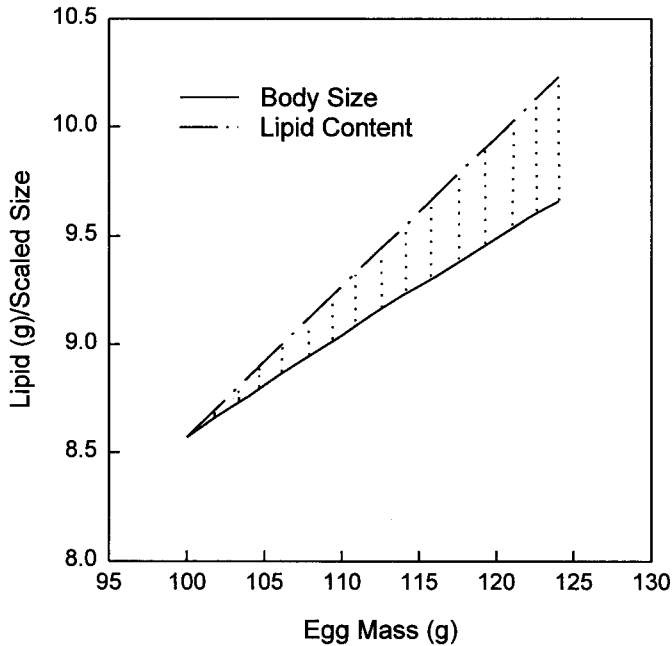


FIGURE 2. Relationship between body size (PC1) and lipid content of neonates relative to egg mass. Dotted region represents excess lipids resulting from larger egg size. Equations for lipid and body size lines were calculated from Snow Goose data (Table 8) with body size intercept adjusted to that of lipid.

egg size and clutch size in geese and found no evidence for facultative manipulation of egg size. In this study, about 95% of the population initiated clutches within 10 days and egg mass did not decline seasonally (Table 2). Geese that lay later adjust initial reproductive effort by varying the number, but not size/mass, of young. However, further adjustments could be made by varying egg quality (*sensu* Ricklefs 1984). In our sample, females that nested later produced eggs with less yolk protein than did those that laid eggs earlier in the season (Table 2). There was, however, no decline in total egg protein (Table 2) and, consequently, gosling nutrients did not vary seasonally. During the first week of embryonic development, yolk is the primary source of protein for structural development (Hazelwood 1972). Therefore, the seasonal decline in yolk protein may have influenced how nutrients were allocated to different protein depots within goslings. In Ross' Geese, dry mass of the pectoralis muscle declined seasonally (Table 3). Development of skeletal muscles is important for thermoregulation (Ricklefs 1983) and, as a result, survival of later-hatched goslings could be compromised under poor environmental conditions,

particularly if female age (experience) covaries negatively with date of nest initiation.

#### EGG MASS AND OFFSPRING QUALITY

Egg size influenced apparent gosling quality. Goslings from heavier eggs had a relative lipid content similar to goslings from lighter eggs but were proportionately smaller in structural size (Table 8, Fig. 2). Egg nutrients varied isometrically with egg size and goslings from larger eggs must have catabolized relatively fewer egg nutrients during embryological development; consequently, for their structural size, goslings from larger eggs hatched with more lipid reserves than did goslings from smaller eggs (Fig. 2). In addition, this relationship could explain the low  $r^2$  value and absence of body size effect for lipids in Table 6. The mechanism for sparing nutrients in goslings from larger eggs is unknown but may be related to constraints on embryonic growth and metabolism.

Although goslings from larger eggs appear to have an energetic advantage over goslings from smaller eggs, the relative quality, *i.e.*, viability, of a gosling should be judged against ecological constraints faced by offspring. Goslings from

larger eggs should have greater thermogenic capacity due to absolutely larger body size and greater nutrient reserve capacities due to proportionally larger fat reserves (Fig. 2) than goslings from smaller eggs. At hatch, inclement weather or poor foraging conditions may preclude feeding by goslings. Neonates with relatively more lipids for their body size may survive better and perhaps continue to grow during periods of thermal and/or nutritional stress. Unfortunately, the lower limit of thermal neutrality is unknown for goslings and specific predictions about the effect of temperature on gosling growth and survival are difficult to make. The hypothesized advantage of larger egg size has been supported by two studies which related egg size to early gosling survival (but see Williams 1994 and citations therein). In Snow Geese, Ankney (1980) found that captive goslings from larger eggs had better fasting endurance than did those from smaller eggs. In the central Arctic, wild Ross' and Snow goslings from large eggs had the highest probability of survival at age 21–33 days (Slattery 1994). Thus under some conditions, heavier eggs confer an advantage to goslings over those from smaller eggs beyond absolutely larger body size (Fig. 2). This effect of egg size on survival may be more important for Ross' goslings that travel farther from the nesting colony and thus may have even higher energetic demands than do Snow goslings (Slattery 1994).

Although goslings from larger eggs appear to survive better under some environmental conditions (Ankney 1980, Slattery 1994), the evolutionary implication of hatching from a large egg is somewhat unclear (Williams et al. 1993, Williams 1994). Traits associated with fitness theoretically should have low heritabilities since selection would rapidly lead to genetic fixation (Falconer 1981). However, egg size in geese is highly heritable (Newell 1988, Lessells et al. 1989, Larsson and Forslund 1992) and therefore could respond to selection (Endler 1986). If, on average, egg size is positively correlated with gosling survival, then directional selection should reduce egg size variability and decrease heritability (Boag and Van Noordwijk 1987). Egg size, however, is highly variable in Snow Geese and selective pressures maintaining this variability are unknown (Ankney and Bissett 1976, Newell 1988, Lessells et al. 1989). Ankney and Bissett (1976) hypothesized that egg size was adapted to "average" environmental conditions and that genetic vari-

ability was maintained by opposing directional selection for either large or small eggs in some years. By definition, Ankney and Bissett's (1976) hypothesis implies weak stabilizing selection which could also reduce variability in egg size (Grant 1986, Newell 1988). Williams et al. (1993), however, found no support for this hypothesis and concluded that egg size per se, had little fitness consequences in southern breeding (La Perouse Bay, MB, 58°43'N, 93°27'W) Lesser Snow Geese. Since egg size was not correlated with body size in that population (Cooch et al. 1992), Williams et al. (1993) suggested that due to physiological constraints associated with egg production and selection on pleiotropic genes which influence egg size, egg size was under no direct selection. Perhaps the potential effects of egg size on offspring survival are expressed only in the short term and are either offset or confounded by parental behavior, e.g., brooding, or become diluted by other mortality factors later in brood rearing (Williams 1994).

#### INTERSPECIFIC VARIATION IN EGG AND GOSLING QUALITY

If egg size influences gosling energetics and subsequent survival under some environmental conditions, then Ross' Geese appear to compensate for smaller egg size by producing goslings with larger protein reserves for their egg size (Table 6), heavier gizzards for their body size (Table 7) and more functionally mature skeletal muscle tissue (Table 5) than do Snow Geese. In addition, Ross' Geese hatch at a relatively larger size when compared to adult body size (Table 10) and thus require less growth to reach asymptotic size (MacInnes et al. 1989). The value of protein as an energy source is somewhat limited because protein contains about half the energy of lipids and is not readily mobilized (Blem 1990). Protein reserves appear to be more important for initial growth than for survival (Duncan 1988), and the advantage of larger protein reserves in Ross' goslings may allow relatively faster early growth than in Snow goslings. These relatively enhanced qualities in Ross' goslings, however, may result at the expense of protracted incubation by nesting females. Ross' Geese incubate longer than do Snow Geese, relative to egg size (both incubate about 22 days, Ryder 1971a, 1972). Therefore, if incubation time increases with egg size (Rahn and Ar 1974), then Ross' Geese trade-off incubation costs by spending

more time fasting but resulting in more developed young at hatch.

Interspecific variation in body size may have important implications for neonate energetics and, thereby, for interpretations of relative offspring quality. Snow goslings are structurally larger and also heavier than Ross' goslings (Table 3). Therefore, Ross' Goose neonates should have a higher mass-specific metabolic rate, larger surface: volume ratio, and, consequently, greater mass-specific energy requirements and higher rates of heat loss than do Snow Geese (Ricklefs 1974, 1983). Indeed, Balmer and Strobusch (1977) hypothesized that surface: volume ratios and subsequent heat loss limit minimum body size of precocial neonates and this limit could be higher in Arctic environments (Koskimies and Lahti 1964). Under nutritional or thermal stress, smaller Ross' goslings could be energetically disadvantaged compared to larger Snow goslings unless they have adaptations which offset size-related energetic costs. Such adaptations apparently exist. Although we did not examine plumage differences (Ricklefs 1983), Ross' Goose neonates appear to be better adapted for nutrient assimilation and thermogenesis judging from their relatively larger gizzards and more functionally mature tissue than Snow Geese. Relatively larger gizzards may indicate a more developed digestive system that allows Ross' goslings to process food quicker and thus assimilate nutrients relatively faster than Snow Geese (Sibley 1981, Sedinger and Raveling 1984, Manseau and Gauthier 1993). In European Starlings, Ricklefs and Webb (1985) demonstrated that the ability to produce heat was inversely related to the fraction of water in muscle tissue, i.e., the functional maturity of muscles (Ricklefs 1983). If true in precocial species, then Ross' Geese should be able to thermoregulate sooner and produce more heat for their body size than Snow goslings.

Although characteristics which offset size-related energetic costs suggest that Ross' goslings can thermoregulate and/or assimilate nutrients more efficiently than Snow goslings, each species likely faces different metabolic constraints. When exposed to similar energetically stressful conditions, Ross' Goose neonates may be disadvantaged compared to Snow Goose neonates, yet Ross' goslings still may have better physiological abilities to produce heat and acquire nutrients than predicted from their body size. We predict

that similar adaptations in digestive efficiency and tissue maturity exist in other Arctic nesting waterfowl, particularly in ducks whose young are as small as, or smaller than, Ross' goslings (Koskimies and Lahti 1964, Robertson and Cooke 1993). These adaptations, however, are likely modified by food type (animal vs. plant material), brood movement patterns, parental behavior and other energetic considerations.

Greater functional maturity of tissues is associated with higher activity levels (King and Farner 1961). If true, then Ross' goslings may demonstrate a greater propensity for activity than do Snow goslings. Broods disperse rapidly soon after hatch and within 17 days, some Ross' broods are nearly 60 km from the colony (Slattery 1994). Ross' broods, on average, travel about 2.5 times farther from the colony than do Snow Goose broods and these dispersal patterns may be related to different habitat requirements (Slattery 1994). Therefore, Ross' goslings may have enhanced physiological adaptations for travel than do Snow goslings.

In summary, examination of egg and gosling composition has provided insight into the role of season, egg and body size, and taxonomy on neonate energetics. Composition of eggs and goslings is similar for Ross' and Snow Geese. We detected seasonal variation in yolk protein, but found no seasonal variation in overall egg or gosling constituents for either species. Intraspecifically, egg size is an important determinant of neonate reserves because larger eggs produce goslings with more lipids for their body size than do smaller eggs. This relationship may explain the higher survival rates observed for goslings from larger eggs (Ankney 1980, Slattery 1994). However, the advantages may be only short-term. Interspecific variation in egg size did not translate into differences in neonate condition. Although interspecific differences in composition of neonates was minimal, Ross' Geese appear to offset energy costs associated with smaller body size by producing neonates with relatively larger gizzards and more functionally mature tissue than that of Snow Geese. The influence of these apparent adaptations for better nutrient assimilation and thermoregulation on survival of hatching Ross' Geese is unknown.

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